

BIOLOGY, ECOLOGY, AND MANAGEMENT OF THE DIAMONDBACK MOTH

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INTRODUCTION

Perspective and History of Pest Status

In recent years, the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae), has become the most destructive insect of cruciferous plants throughout the world, and the annual cost for managing it is estimated to be U.S. \$1 billion (168). Members of the plant family Cruciferae occur in temperate and tropical climates and represent a diverse, widespread, and important plant group that includes cabbage, broccoli, cauliflower, collards, rapeseed, mustard, and Chinese cabbage, the most important vegetable crop grown in China (90), the most populous country in the world. Although the diamondback moth is believed to have originated in the Mediterranean area (64), the source of some of our most important crucifers (185), diamondback moths now occur wherever crucifers are grown, and this insect is believed to be the most universally distributed of all Lepidoptera (107).

Absence of effective natural enemies, especially parasitoids, is believed to be a major cause of the diamondback moth's pest status in most parts of the world (92). Lack of parasitoids in a particular area may have occurred because the diamondback moth is better able than its natural-enemy complex to become established in newly planted crucifers. Reports on the ability of diamondback moths to migrate long distances are numerous (19, 40, 54, 58, 108, 120,

183), but there is no record of migration of any of its parasitoids. Another reason for the lack of effective biological control in an area may be destruction of natural enemies by the use of broad-spectrum insecticides. Prior to the introduction of synthetic insecticides in the late 1940s, diamondback moths were not reported as major pests of crucifers. However, with widespread use of synthetic insecticides on crucifers beginning in the mid 1950s, important natural enemies were eliminated. This event, in turn, led to continued use of synthetic insecticides and eventual insecticide resistance and control failures. In 1953, the diamondback moth became the first crop pest in the world to develop resistance to DDT (7, 83), and now in many countries the diamondback moth has become resistant to every synthetic insecticide used against it in the field (174, 175). In addition, diamondback moths have the distinction of being the first insects to develop resistance in the field to the bacterial insecticide *Bacillus thuringiensis* (62, 86, 151, 164). Insecticide resistance and control failures are now common in tropical climates such as parts of Southeast Asia, Central America, the Caribbean, and the southeastern United States. In some of these areas, economical production of crucifers has become impossible, a situation similar to the demise of the cotton industry in parts of Central America (106).

This review provides the reader with a global overview of the biology and ecology of the diamondback moth, its association with its host plants and natural enemies, and past, present, and future management strategies. We give an overview of the characteristics of diamondback moths and past management practices that resulted in widespread control failures, and we provide perspectives intended to improve management in the future. This review does not contain all references to diamondback moths but does provide what we consider to be the most relevant work pertaining to each area we discuss.

Sources of Information

The diamondback moth was the subject of two widely attended international workshops in Taiwan, and the proceedings of those meetings (168, 170) are important sources of information. The first volume of an annotated bibliography compiles most of the literature published until mid 1985 (175). A second volume covers those papers published between December 1985 and September 1990 (174). All literature published in Japanese until 1988 was recently compiled by a group of Japanese entomologists (138). The library of the Asian Vegetable Research and Development Center (AVRDC) in Taiwan contains a complete data base and collection of reprints for the diamondback moth. These resources are available free of charge to scientists interested in diamondback moth research.

Host Range and Host Specificity

The diamondback moth feeds only on members of the family Cruciferae. Members of this diverse plant group are cultivated for various edible plant

parts, such as the roots of radishes and turnips, the stems of kohlrabi, the leaves of cabbage and other leafy brassicas, and the seeds of mustard and rape, which are consumed as fresh, cooked, or processed vegetables. Crucifers are grown in tropical and temperate climates and in a variety of cropping systems from backyard gardens to large-scale fully mechanized farms. Crucifers are the most common vegetables in the diet of Asians and are important components in the diets of most other cultures. The 1990 Food and Agriculture Organization of the United Nations (FAO) production figures (53) indicate that, on a worldwide basis, cruciferous vegetables were grown on 2.2×10^6 ha with half this production occurring in Asia. When rapeseed acreage is added to the above figure, it exceeds 17.6×10^6 ha.

Cultivated crops on which the diamondback moth feeds include cabbage (*Brassica oleracea* var. *capitata*), cauliflower (*B. oleracea* var. *botrytis*), broccoli (*B. oleracea* var. *italica*), radish (*Raphanus sativus*), turnip (*B. rapa* *pekinensis*), Brussels sprouts (*B. oleracea* var. *gemmifera*), Chinese cabbage (*B. rapa* cv. gr. *pekinensis*), kohlrabi (*B. oleracea* var. *gongyloides*), mustard (*B. juncea*), rapeseed (*B. napus*), collard (*B. oleracea* var. *acephala*), pak choi (*B. rapa* cv. gr. *pakchoi*), saishin (*B. rapa* cv. gr. *saishin*), watercress (*Nasturtium officinale*), and kale (*B. oleracea* var. *alboglabra*). In addition, the diamondback moth feeds on numerous cruciferous plants that are considered to be weeds. The diamondback moth maintains itself on these weeds only in the absence of more favored cultivated hosts. The following crucifers have been reported to sustain feeding and reproduction of diamondback moth: *Arabis glabra*, *Armoracia lapathifolia*, *Barbarea stricta*, *Barbarea vulgaris*, *Basella alba*, *Beta vulgaris*, *Brassica caulorapha*, *Brassica kaber* (- *Sinapis arvensis*), *Brassica napobrassica*, *Bunias orientalis*, *Capsella bursa-pastoris*, *Cardamine amara*, *Cardamine cordifolia*, *Cardamine pratensis*, *Cheiranthus cheiri*, *Conringa orientalis*, *Descurainia sophia*, *Erysimum cheiranthoides*, *Galinsoga ciliata*, *Galinsoga parviflora*, *Hesperis matronalis*, *Iberis amara*, *Isatis tinctoria*, *Lepidium perfoliatum*, *Lepidium virginicum*, *Lobularia maritima*, *Mathiola incana*, *Norta* (*Sisymbrium*) *altissima*, *Pringlea antiscorbutica*, *Raphanus raphanistrum*, *Rorippa amphibia*, *Rorippa islandica*, *Sinapis alba*, *Sisymbrium austriacum*, *Sisymbrium officinale*, and *Thlaspi arvense* (38, 56, 65, 85, 96, 109, 129). Alternate weed hosts are especially important in maintaining diamondback moth populations in temperate countries in spring before cruciferous crops are planted.

The host range of diamondback moths is limited to crucifers that contain mustard oils and their glucosides (60, 61, 71, 113, 181, 182). Many glucosinolates stimulate feeding in diamondback moths, but two of these (3-butenyl and 2-phenylethyl) are toxic to them at high concentrations (113). The glucosides sinigrin, sinalbin, and glucocheirolin act as specific feeding stimulants for diamondback moths, and 40 plant species containing one or more of these chemicals serve as hosts. Nonhost plants may contain these stimulants but also contain feeding inhibitors or toxins (60). Certain chemicals

such as sulfur-containing glucosinolate or its metabolites, allyl isothiocyanates, are present in crucifers and act as oviposition stimulants (61, 130). Sulfur-deficient plants are not attractive to diamondback moths for oviposition (61). At a subcellular level, the oviposition-stimulating activity of glucosinolates can be eliminated by treatment with myrosinase or sulfatase enzymes that degrade glucosinolates (130). The oviposition-inhibiting property of coumarin present in *Melilatus* spp. can be overcome by treatment with allyl isothiocyanate, but application of this compound could not reverse the similar property of an unknown substance in tomato leaf (61). Allyl isothiocyanate also stimulates egg production in diamondback moth adults (70). Recent studies indicate the presence of unidentified olfactory stimuli that attract diamondback moths to crucifers (121, 125).

BIOLOGY AND ECOLOGY

General Life Cycle

Diamondback moth adults become active at dusk and continue so into the night (64). Most adults emerge during the first 8 h of photophase (124), and mating occurs at dusk of the same day the adults emerge. Female moths start laying eggs soon after mating, and the oviposition period lasts 4 days, during which the female lays 11–188 eggs (64). The majority of eggs are laid before midnight with peak oviposition occurring between 7:00 and 8:00 PM (11, 124). The ratio of eggs laid on the upper and lower leaf surfaces is approximately 3:2; very few eggs are laid on stems and leaf petioles (10, 64). Eggs are laid preferentially in concavities of leaves rather than on smooth surfaces (61). Lack of light during normal daylight stimulates oviposition, but light during night hours does not completely inhibit it (11, 163). Plant volatiles, secondary chemicals, temperature, trichomes, and waxes on leaf surfaces all influence oviposition (9, 98, 125, 163, 187). The incubation period, which is influenced mainly by temperature, lasts 5 to 6 days.

Soon after emergence, neonate larvae start feeding on foliage. The first-instar larvae mine in the spongy mesophyll tissue, whereas older larvae feed from the lower leaf surface and usually consume all tissue except the wax layer on the upper surface, thus creating a window in the leaf. The duration of the four larval instars depends on temperature (18, 77, 98, 140, 141). In 1022 observations during summer in Ontario, Canada, the average duration of the larval instars was 4.0, 4.0, 5.0, and 5.6 days for the first through fourth instars, respectively (64). Faster developmental times are reported in warmer climates, and the host crop also influences development rates (74).

When the fourth-instar larva has completed its feeding, it constructs an open-network cocoon on the leaf surface where it fed and spends a two-day

period of quiescence marking the prepupal stage. The prepupa sheds its larval skin, which remains attached to the caudal end of the pupa. The duration of the pupal period varies from 4 to 15 days depending on temperature (1, 23, 65, 74, 97). Adult moths emerge primarily between 1:00 and 4:00 PM with a peak at 2:00 PM (124, 139). Adults feed on water drops or dew and are short lived.

Relationship with Environmental Factors

DIAPAUSE Whether the diamondback moth diapauses or hibernates in any of its life stages is a controversial topic. In the tropics and subtropics where crucifers are grown throughout the year, all life stages of diamondback moth can be present at any time. In temperate regions where crucifers are not grown year-round, the diamondback moth's perennial occurrence has led several researchers to believe pupae and/or adults hibernate in host-plant debris through the winter (16, 105, 108, 147, 178, 186). However, in none of these studies were insects collected during the coldest months and brought out of hibernation. A single study at Ithaca, New York mentions the presence of motionless diamondback moth adults in crop remnants in the field (64), but it was not clear whether they would have survived the winter. In a study in upstate New York (A. M. Shelton, unpublished results), no diamondback moth pupae survived the winter, and when moth activity was monitored throughout the year using pheromone traps, no moths were caught during the winter months of 1990–1991 despite several warm spells lasting for several days. During the same winter in Long Island, New York, however, moths were captured.

The origin of diamondback moths in an area and their ability to survive in that area during noncropping periods remains an important question. Insecticide-resistant diamondback moths that can overwinter may pass genes for resistance to subsequent generations, but if no overwintering occurs, genes for resistance will be lost in that area unless new resistant individuals arrive. Future research on overwintering may give more definitive information; for the present, however, we assume that the diamondback moth does not overwinter in many temperate areas where it is a pest and that immigration occurs by the adult moths moving on wind currents or by all stages arriving on contaminated seedlings.

MIGRATION Among the various criteria that make the diamondback moth one of the most cosmopolitan pests is its ability to migrate and disperse over long distances. In Britain, where mass migration of diamondback moths has been studied extensively, the yearly occurrence of diamondback moths is attributed to migration by adults from the Baltic and southern Finland, a distance >3000 km (40, 58, 102, 108, 120, 178). These studies indicate that

moths can remain in continuous flight for several days and cover distances of 1000 km per day, but how the moths survive at such low temperatures and high altitude is not known. In eastern Canada, annual populations of diamondback moths originate by adult migrations from the United States (67, 152). Similarly in Japan, this insect migrates from southwestern islands, some of which are warm subtropical, to the cooler temperate climate of Honshu and Hokaido (73). Similar migrations probably occur in other parts of the world such as New Zealand, Australia, South Africa, and southern parts of Chile and Argentina.

In recent years in the United States, use of seedlings grown in the southern states contaminated with diamondback moths has proven to be a major source of diamondback moth infestations in northern states (151). High levels of seedlings contaminated with diamondback moth larvae that are resistant to many insecticides has led to major control failures in several states (151).

MANAGEMENT

Present Management Practices

SMALL-SCALE FARMING In developing countries of the tropics and subtropics, production of crucifers is characterized by small farms and intensive use of land, labor, and pesticides. Because of the need to produce fresh vegetables for residents of large cities on a daily basis, farms are usually located on the outskirts of such population centers or in cleared areas in the highlands with easy access to cities. Cultivation of fresh crucifers is an important source of income, and production of healthy looking, damage-free vegetables for the relatively wealthy city dwellers is an important consideration in all cultivation practices, especially plant protection. The mainstay of control is the frequent use of insecticides, often applied with backpack sprayers with few safety features to the applicator. In most developing countries, introduction of insecticides, all of which are imported from developed countries, face little, if any, registration hurdles common in the West and Japan. As a result, most insecticides, some of which are not registered in the country of origin, are readily available at a reasonable cost. In some countries, pesticides are subsidized, especially for staple foods such as rice and export crops such as cotton, and because of the absence or poor enforcement of restrictions on pesticide use, insecticides registered for rice and cotton are often applied to cruciferous vegetables. All these factors contribute to the overuse and complete dependence on insecticides to control diamondback moth. Tropical countries where crucifers are grown throughout the year may see 20 diamondback moth generations per year, and the sole reliance on insecticides for control facilitates the rapid buildup of resistance. It is no coincidence that

the first report of diamondback moth resistance to an insecticide in 1953 came from one intensive production area in the tropics, Indonesia (7, 83), decades before the appearance of resistance even in the warm areas of the continental United States (89, 104, 151), Hawaii (165), or Japan (8, 184). To overcome resistance, farmers often increase doses of insecticides, use mixtures of several chemicals, and spray more often, sometimes once every two days. In most of these areas, the insecticide cost amounts to between 30 and 50% of the cost of production, well above the fertilizer cost (91). These high levels of use have caused the diamondback moth to become resistant to practically all insecticides in many areas. Additionally, high insecticide use has led to excessive residues on produce. Because pesticide-residue monitoring is absent or not enforced, insecticide-contaminated crucifers often pass easily through marketing channels.

Because of the lack of proven alternatives and the continued availability of relatively cheap insecticides, insecticides remain the main control tactic. In a few countries such as Malaysia, Indonesia, and the Caribbean islands, alternative control tactics such as introduction of parasitoids have been tried (92), but the success of these efforts has been thwarted by the continuing indiscriminate use of synthetic insecticides. An Asian IPM program to combat diamondback moth through the use of natural enemies and judicious use of insecticides is now financed by the Asian Development Bank, but years will pass before benefits of this effort are realized. Similarly, the International Atomic Energy Agency has initiated a cooperative study in Malaysia and Indonesia to assess the possibility of managing diamondback moths with a sterile-insect program.

LARGE-SCALE FARMING In developed countries, production of crucifers is characterized by large-scale farming practices, which include the reduction of labor, the increase of management and capital, and the consolidation of land into larger holdings. Large-scale farming of crucifers is common in North America and Europe and is becoming increasingly common in Mexico and Central America. In these areas, crop-protection decisions tend to be similar over relatively large areas. The primary method of control of diamondback moths in large-scale farming involves insecticides applied by air or ground rigs. In North America, Europe, and New Zealand, researchers have incorporated insecticides into IPM programs that utilize scouting and threshold strategies (15, 21, 75, 76, 146, 149, 179). In the United States, management of the diamondback moth was not difficult until the mid 1980s, but then control failures occurred in Hawaii (165), Texas (104, 126), Florida (80–82, 89), and eventually throughout North America (151). Several factors caused this rapidly occurring set of control failures, including the relatively warm growing seasons during the mid 1980s that led to an increase in the number

of generations produced; the lack of rainfall, a major mortality factor for diamondback moth (64); the recent shift to a shorter or nonexistent crucifer-free period in southern states; the movement of contaminated transplants within and between states; and the development of resistance. In several areas of the United States where resistance is high, especially Florida, the frequent use of insecticides and lack of adequate control has made crucifer production often unprofitable. In other parts of the world (e.g. Europe and New Zealand), control still appears to be adequate.

There is a movement throughout the developed countries to reduce pesticide use. Several northern European countries have mandated, or are in the process of mandating, a 50% reduction in the use of synthetic pesticides by the year 2000; other countries will likely follow this lead. To achieve this end and still produce acceptable-quality crucifers, crop-protection entomologists must come up with alternatives to the sole reliance on synthetic insecticides. In many areas of the world where control problems are most acute, growers are presently testing such tactics as inoculative releases of parasitoids, conservation of natural enemies, mating disruption, and cultural controls.

Cultural Control

Because of the failure of insecticides to control the diamondback moth, interest is growing in cultural controls in commercial crucifer production. Some of the classical control measures that have been tried with some success are intercropping, use of sprinkler irrigation, trap cropping, rotation, and clean cultivation.

INTERCROPPING Intercropping, the practice of growing two or more crop species together, is a normal cultivation practice in the tropics where farms are small and land is used intensively. However, in these areas intercropping is not presently used for management of diamondback moths, but rather for horticultural and economic reasons. For some crop-insect situations, intercropping has reduced pest populations because the plants act as physical barriers to the movement of pest insects, because natural enemies are more abundant, and/or because the chemical or visual communication between pest insects and their host plants is disrupted (133, 135, 148). The earliest successes occurred in Russia where intercropping cabbage with tomato reduced damage to cabbage by several pests, including the diamondback moth (190). This practice, however, had only limited success in India (23, 153), the Philippines (103), and Taiwan (11). At the last location, none of the 54 crops tested for their utility in intercropping had any significant impact on the population of diamondback moth on cabbage. Intercropping with *Salvia officinalis*, *Thymus vulgaris*, and *Trifolium repens* consistently reduced damage to Brussels

sprouts from diamondback moth (44, 45), but these crops would not be economically suitable for most small farmers.

SPRINKLER IRRIGATION All but the first-instar larvae of the diamondback moth are exposed on the leaf surface and influenced by various abiotic factors. Several reports indicate that rainfall is an important mortality factor for diamondback moths (22, 26, 58, 59, 64, 66, 85, 171, 191), and thus, it is only a serious pest during the dry season. Overhead irrigation has been shown to reduce diamondback moth injury in cabbage (11, 172) and watercress (112, 166). The sprinkler drops are believed to drown or physically dislodge the insect from the plant surface, which causes this reduction. This operation at dusk also reduced mating-related flight activity (12) and presumably oviposition. Using sprinkler irrigation to control diamondback moth in crops other than watercress, however, is not practical on a commercial farm because of the high cost and probable increase of diseases such as black rot and downy mildew.

TRAPCROPPING Before the advent of modern organic insecticides, a common practice was to plant strips of an economically less important plant highly preferred by the diamondback moth within a commercial crucifer field. The preferred crops, primarily white mustard (*Brassica hirta*) or rape (*B. juncea*), attracted diamondback moths, which spared the commercial crop, such as cabbage, Brussels sprouts, and others, from its attack (56, 84, 131). Now that the same modern insecticides that made past trap-cropping practices obsolete are made obsolete by insecticide resistance, trap cropping is becoming a more realistic alternative, especially in developing countries. In India when mustard was alternated with every 15 to 20 rows of cabbage, diamondback moths colonized the mustard and spared the main cabbage crop (154). In order to trap most immigrating diamondback moth adults in a field, mustard must be available throughout the cabbage growing period. Effective trap cropping may eliminate all insecticides because diamondback moth larvae are retained in the trap crop and become heavily parasitized. This cultural control practice is now expanding rapidly in India.

ROTATION AND CLEAN CULTIVATION Crop rotation is rarely practiced for control of diamondback moth populations in intensive vegetable growing areas of the tropics and subtropics because of the high prices that crucifers fetch. However, because continuous planting of crucifers allows continuous generations of diamondback moth, which leads to frequent use of insecticides and the development of resistance, crop rotation may become a necessity.

Clean cultivation can be an important factor in the management of diamondback moth. Planting seedbeds away from production fields, and plowing down crop residues in seedbeds and production fields is an efficient

and easy management practice. Where transplants are grown in the greenhouse, prevention of infestations by immigrating adults can be accomplished through the use of screening. Frequent insecticide spraying is common for control of greenhouse infestations, but this may lead to insecticide resistance (62, 151). Alternative strategies such as plant resistance, use of pheromone disruption, biological control, and other tactics should be investigated.

Plant Resistance

Several studies have surveyed existing germplasm for resistance to Lepidoptera, including the diamondback moth, in crucifers (20, 39, 42, 43, 46, 69, 123, 128, 150). The most notable resistance came from germplasm in the United States Northeastern Plant Introduction Station. Two types of resistance have been identified from material in this collection (48). In two normal bloom cabbage types, resistance is chemically based and elicits antibiosis or nonpreference in the larvae. Polar fractions of ethanol extracts from these types, when incorporated into an artificial diet, caused levels of mortality similar to those observed with intact plants in the field. However, mortality on these types was much lower than on glossy type cabbages derived from a cauliflower accession (PI 234599). Whole-leaf ethanol extracts of glossy types had no activity in the diet, and further studies indicated that resistance resulted from a change in behavior by neonate larvae (48) caused by differences in the amount and chemical composition of leaf-surface waxes (49, 47a). Recent work indicates that application of *s*-ethylthioproprylthiocarbamate to normal bloom cabbages changes the leaf-surface waxes to ones similar to those of the genetic glossy type, and these cabbages thereby become resistant to diamondback moth neonate larvae (47). Chemically induced glossiness may have tremendous potential as an economic control of diamondback moth and as a method of assisting insecticide-resistance management strategies.

The glossy leaf trait derived from PI 234599 is inherited as a simple recessive gene. Cabbage lines derived from this parent have been successfully tested in Honduras under extreme pest pressure and provided >95% control (42). Other genes for glossiness were examined for insect resistance (155, 156), and the results indicated high levels of resistance and that leaf-surface waxes caused the resistance (49). Especially important are recent results indicating that high levels of resistance can be obtained from glossy dominant genes (155). Currently, two major seed companies are developing glossy lines for resistance to diamondback moths (A. M. Shelton, unpublished data).

Sex Pheromone

Evidence for sex pheromone emission in female adults of diamondback moths was initially demonstrated in Taiwan (31). The pheromone consists of three components, (*Z*)-11-hexadecenal (*Z*-11-16:Ald), (*Z*)-11-hexadecenyl acetate (*Z*-11-16:OAc), and (*Z*)-11-hexadecenyl alcohol (*Z*-11-16:OH) (5, 29, 35),

and is now available commercially. The exact proportion of the three components in a pheromone blend that will attract the maximum number of male moths is influenced mainly by air temperature and possible strain differences in female response that might occur at widely spaced locations, but not by humidity (99). Extensive studies have been conducted to determine the optimal proportion and loading of the pheromone components, effect of environmental factors, effective distance, longevity, etc (27–29, 32–36, 88, 94, 99–101) in order to use the pheromone more effectively in the field. The pheromone has been used for monitoring diamondback moth populations in the field (13, 88), and during the past three years, Japanese scientists have succeeded in achieving mating disruption in cabbage fields using high concentrations of the pheromone (114–116). A 1:1 mixture of (*Z*)-11-16:Ald and (*Z*)-11-16:OAC, known as KONAGA-CON, is now commercially available in Japan. Collaborative multilocation studies in that country have shown promising results (115), but KONAGA-CON's use is still not cost effective. J. R. McLaughlin and his colleagues in Florida have used a two-component pheromone blend in a "continuous rope formation" (Shin-Etsu Chemical Co.) for mating disruption and demonstrated suppression of mating activity. This tactic may hold the most promise when used in combination with the augmentation or conservation of natural enemies.

Biological Control

All stages of diamondback moth are attacked by numerous parasitoids and predators with parasitoids being the most widely studied. Additionally, adults are often attacked by polyphagous predators such as birds and spiders. Although over 90 parasitoid species attack diamondback moth (57), only about 60 of them appear to be important. Among these, 6 species attack diamondback moth eggs, 38 attack larvae, and 13 attack pupae (92). Egg parasitoids belonging to the polyphagous genera *Trichogramma* and *Trichogrammatoidea* contribute little to natural control and require frequent mass releases. Larval parasitoids are the most predominant and effective. Many of the effective larval parasitoids belong to two major genera, *Diadegma* and *Cotesia* (= *Apanteles*); a few *Diadromus* spp., most of which are pupal parasitoids, also exert significant control. The majority of these species came from Europe where the diamondback moth is believed to have originated. In Moldavia in Romania, 25 species of parasitoids occur and parasitize 80–90% of diamondback moths (111).

Southeast Asia, the Pacific islands, Central America, the Caribbean, and most of sub-Saharan Africa are most intensively plagued by diamondback moths because these areas lack effective larval parasitoids. This contrasts with countries in continental Europe and North America, which are endowed with many *Diadegma*, *Cotesia*, and *Diadromus* spp.

PARASITOID INTRODUCTIONS Introduction of exotic parasitoids to control pest insects and weeds has been practiced for decades (41, 78, 160). This approach has considerable promise in the control of diamondback moths; however, it has been practiced only sporadically over the past 50 years. Widespread and often indiscriminate use of insecticides has frustrated recent efforts and delayed the establishment of parasitoids and their beneficial effects.

One of the earliest parasitoid introductions was made in New Zealand. When no significant parasitism of diamondback moths by three native larval-parasitoid spp. was found (110, 134), *Diadegma semiclausum* and *Diadromus collaris* were introduced to New Zealand from England (68, 180). These introductions continue to suppress diamondback moth populations, and the challenge today is to incorporate this natural control into a commercial IPM program (15).

A somewhat similar situation existed in Australia where, prior to the introduction of effective exotic parasitoids, diamondback moths caused serious damage (192). Among the introduced parasitoids, *D. semiclausum* became established throughout Australia, including Tasmania. *Diadromus collaris* was established principally in Queensland, New South Wales, Victoria, and Tasmania, and *Cotesia plutellae* was established in Australian Capital Territory, New South Wales, and Queensland. These introductions resulted in heavy parasitism of diamondback moth (72–94%) and marked reduction in damage to crucifers (57, 63, 192).

Efforts to control diamondback moths in Indonesia by introduction of parasitoids were initiated in 1928 (50). However, only in the early 1950s was the exotic parasitoid *D. semiclausum* actually introduced from New Zealand into the crucifer-growing areas in the highlands of Java, where it became established (189). Because of overuse of insecticides, the beneficial effects of this parasitoid in the control of diamondback moths in the field were not realized until mid 1980s (143). With the substitution of *B. thuringiensis* in the early 1980s, the parasitoids proliferated (143). This parasitoid has now been introduced from Java to the highlands of other islands in Indonesia.

An identical situation existed in the Cameron Highlands of Malaysia, the major vegetable-production area for Malaysia and Singapore, where crucifers are grown year round and the diamondback moth is a serious pest. Prior to 1977 only one parasitoid, *Tetrastichus ayyari*, was present in this area, but it did not adequately suppress diamondback moth populations (91, 117). Malaysian entomologists in 1977–1978 introduced one larval parasitoid, *D. semiclausum*, and two pupal parasitoids, *Tetrastichus sokolowaskii* (= *Oomyzus sokolowaskii*) and *D. collaris*, into this area (119). Although these parasitoids were recovered from diamondback moths in the Cameron Highlands one and six years after the release, parasitism was only 6% for both *D. semiclausum* and *D. collaris*. *Tetrastichus sokolowaskii* (= *Oomyzus sokolowaskii*) was recovered in 1978 but was not found in 1984 (37). Parasitism by *C. plutellae*,

which entered this area accidentally (91), amounted to 11% in 1978 and 20% in 1984. Because insecticides were still effective, farmers continued to use them intensively, which kept the parasitoid population very low. Toward the end of the 1980s, however, diamondback moths developed resistance to practically all synthetic insecticides, and officials in Singapore, the major market for vegetables grown in Cameron Highlands, rejected cabbage because of high insecticide residues. These two events forced farmers to start using *B. thuringiensis* (118), resulting in an increase in the parasitoid population and reduced diamondback moth damage. Surveys in 1989 showed that *D. semiclausum* and *D. collaris* have become the dominant parasitoids with *C. plutellae* contributing little control. The combined parasitism has drastically reduced the need for insecticide applications, and cabbage production is increasing (162).

In 1970, *C. plutellae* obtained from India was released in the Caribbean countries of Grenada, St. Vincent, St. Lucia, Dominica, Antigua, Montserrat, St. Kitts-Nevis, Belize, Trinidad, Barbados, and Jamaica. In some of these release sites, the parasitoid has been recovered, but it appears to affect diamondback moth suppression little. Attempts to introduce *C. plutellae* and *D. collaris* were not successful (17, 194). Reintroduction of *C. plutellae* into Jamaica in early 1989 resulted in its establishment; parasitism increased from 5.4% in the first generation following introduction to 88.7% by March of 1990. This parasitism reduced plant damage from 75% before introduction to 38% in March 1990 (3). On the Cape Verde Islands off Africa, locally occurring predators and parasitoids could not control diamondback moths (93). Introduction of *C. plutellae* and *T. sokolowaskii* (= *O. sokolowaskii*) and the use of *B. thuringiensis* resulted in the establishment of these parasitoids and control of diamondback moths (188).

In Taiwan, the diamondback moth has been a serious problem since the mid 1960s (24). *Cotesia plutellae*, reported to parasitize diamondback moth since at least 1972 (30), could not give adequate control, so *D. semiclausum* was imported from Indonesia and released in the lowland crucifer-growing areas in 1985 (9); however, it failed to become established. When broad-spectrum insecticides were replaced by *B. thuringiensis*, *C. plutellae* became established and provided adequate control, but *D. semiclausum* still did not become established (167). However, when *D. semiclausum* was introduced in the highlands, within one season it parasitized >70%, and towards the end of that season diamondback moths could not be found in the field (12). *Diadegma semiclausum* now occurs throughout the highland areas of Central Taiwan and provides substantial savings in diamondback moth control (169, 176). Differential establishment of these parasitoids in highland and lowland areas appears to result from their different temperature requirements. Laboratory studies indicate a temperature range of 20–30°C is optimum for parasitization of diamondback moth by *C. plutellae* and 15–25°C for *D. semiclausum*

(173). At temperatures approaching 30°C, parasitism by *D. semiclausum* drops sharply. In tropical and subtropical areas, only temperatures in the highlands are suitable for the establishment of *D. semiclausum*, whereas temperatures in the lowlands are suitable for *C. plutellae* (169). These studies help explain the successful establishment of *D. semiclausum* in the highlands of Indonesia, Malaysia, and Taiwan and *C. plutellae* in the lowlands of the latter two countries.

In the highland areas of the northern Philippines, a single release of *D. semiclausum* in 1989 at the beginning of the season resulted in 64% parasitism of diamondback moths at harvest (127). The ideal temperature range of 12–28°C most of year in this area is expected to help in the spread of *D. semiclausum* in the remaining crucifer areas in this region.

Insecticides

CHEMICAL-USE PATTERNS Because diamondback moth larvae feed on cruciferous vegetables, which usually have high cosmetic standards, effective control is necessary. Historically, the mainstay of control has been the use of synthetic insecticides. In a review of publications on diamondback moth (175), nearly a third of the papers focused on insecticidal control, and the majority of these involved screening compounds.

General use patterns of insecticides vary widely over geographic locations and decades. The driving forces behind these changing patterns are the development of new, more effective insecticides and the lost usefulness of older insecticides because of resistance. The most dramatic patterns have occurred in Southeast Asia where diamondback moths are abundant. The best example of the rapid change in use patterns is illustrated by Rushtapakornchai & Vattanatangum (136), who compiled a list of screening results in Thailand from 1965 to 1984. A dominant product like mevinphos provided excellent control in 1965, fair control in 1974, and poor control in 1984. In 1976, permethrin was introduced and provided excellent control in the central region, but provided only fair control two years later. In the early 1980s, insect growth regulators (IGRs) were introduced. IGRs, like triflumuron, provided good control in 1982 but poor control by 1984. Other biologicals like *B. thuringiensis* were introduced in the early 1970s and provided fair to good (but never excellent) control when they were first introduced. Because of the lack of excellent control when used alone, *B. thuringiensis* has been used primarily in IPM programs that use thresholds and conserve natural enemies.

Reports from Thailand on the introduction and eventual failure of many insecticides (136, 195) are not unique. Similar patterns have also been documented in other parts of the world such as Taiwan (159), Japan (62), Malaysia (161), the United States (80, 89, 104, 126, 151, 165), and Central America (6). Because of the magnitude of the diamondback moth problem

and the worldwide importance of cruciferous vegetables, new potential control agents such as genetically improved strains of *B. thuringiensis*, neem (145), macrocyclic lactones (2, 51, 161), baculoviruses (79), and fungi (132) are being explored. However, as with all previously used methods, the long-term effectiveness of these agents is questionable because of potential resistance.

INSECTICIDE RESISTANCE Factors that influence the development of resistance in diamondback moths include high fecundity and reproductive potential, rapid turnover of generations, a long growing season, extensive acreage of crucifers, and frequent insecticide applications (104, 159, 193).

Diamondback moths have a long history of eventually becoming resistant to every insecticide used extensively against them. In 1953, Ankersmit (7) noted the development of resistance to DDT in Lembang, Indonesia. Subsequently, the diamondback moth has become resistant to most of the other major classes of insecticides used in Indonesia. In the Philippines, Barroga (14) first reported the development of resistance by diamondback moths in 1974 when she confirmed field failures with EPN and mevinphos. In Malaysia, diamondback moths have become resistant to all groups of conventional insecticides (161). Additional reports from Taiwan (25, 159), Japan (62, 177), Australia (4), and North America (104, 151, 165) have documented resistance to a variety of insecticides. Several authors have reported success with tank mixes once resistance has occurred (81, 89), but the long-term usefulness of this strategy is questionable.

As a first step in managing resistance, Magaro & Edelson (104) developed a technique using disposable cups in which larvae were exposed to discriminating doses of several insecticides at the LC₉₀ level. Such techniques can be used to identify populations resistant to specific insecticides and enable growers to use alternatives, if they are available. Understanding the genetics, field dynamics, mechanisms, and stability of resistance is necessary if resistance management is to succeed, but too often these studies are done once resistance has already developed. Sun (158) summarizes studies on the mechanism(s) of resistance to carbamate, organophosphate, pyrethroid, abamectin, and benzoylphenyl urea (BPU) insecticides in diamondback moths.

Insect-growth regulators and pathogens offer promise as alternatives to broad-spectrum insecticides, which often disrupt the control exerted by natural enemies. Products such as BPU that interfere with chitin synthesis provide an alternative to the more common classes of insecticides and may help in resistance management. However, unofficial reports from Thailand indicate the diamondback moth has already developed significant resistance to several BPUs only 2–3 years after their introduction (122). Additional studies indicated that insects collected from Thailand in 1988 showed resistance to several IGRs including chlorfluazuron, diflubenzuron, hexaflumron, and several experimental IGRs. Resistance presumably resulted from a recessive

monofactorial and autosomal gene. Rearing populations for 40 generations did not result in loss of resistance (87).

Bacillus thuringiensis offers tremendous hope for diamondback moth control because of its specificity and the fact that no serious control failures in the field have been documented despite the use of *B. thuringiensis* for >20 years (55). However, Kirsch & Schmutterer (86) found low efficacy of *B. thuringiensis* control of diamondback moth in the Philippines and speculated that this may have resulted from resistance. Tabashnik et al (164) reported results on populations of diamondback moth collected from commercial fields of watercress, cabbage, and broccoli in Hawaii. In laboratory bioassays, diamondback moths collected from watercress fields that had been heavily treated with *B. thuringiensis* exhibited LC₅₀ and LC₉₅ values 25–33 times greater than those of two susceptible laboratory colonies. In 1990, Shelton & Wyman (151) collected 11 populations of diamondback moths from *Brassica* plants in 6 states and Indonesia and tested for their responses to 2 natural formulations of *B. thuringiensis* and to a genetically engineered form of the bacterial preparation. High levels of resistance (>200-fold) were found in populations that originated from Florida. Additional field studies conducted in 1992 (A. M. Shelton, unpublished results) have documented control failures in several locations in Florida of commercial formulations of *B. thuringiensis* subspecies *kurstaki*: and laboratory assays of these same populations have documented LC₅₀ values greater than 1000-fold. In these same locations, field tests with a formulation of *B. thuringiensis* subspecies *aizawai* provided adequate control, and laboratory assays indicate less than 10-fold variation in LC₅₀ values. Populations that had high LC₅₀ values originated from fields in which *B. thuringiensis* had been used extensively. Hama (62) found high levels of resistance to *B. thuringiensis* in glasshouses in Osaka where watercress had been grown throughout the year. These studies demonstrate that with frequent foliar applications of available *B. thuringiensis* products, resistance to and control failures of the HD-1 isolate of the *kurstaki* serotype of *B. thuringiensis* will occur in the field.

Resistance to *B. thuringiensis* is thought to occur because the crystal does not bind to the brush-border membrane, either because of strongly reduced binding affinity or the complete absence of the receptor molecule (52). Recent studies (C. W. Hoy, unpublished data) indicate that larvae do not avoid droplets containing *B. thuringiensis* on treated foliage but do consume less foliage after they ingest the droplets. B. E. Tabashnik and coworkers (166a) conducted a genetic analysis that indicates that resistance to *B. thuringiensis* was autosomal, recessive, and controlled primarily by one or a few loci. The current *B. thuringiensis* products registered in the United States for diamondback moth control contain only the HD-1 isolate of the *kurstaki* serotype, and that isolate contains only the Cry IA and Cry II toxins (72). A recent report

from Malaysia (161) indicated that a diamondback moth population that had a resistance ratio of 112 to the HD-1 isolate of the *kurstaki* serotype had a resistance ratio of only 3.3 to a product containing the *aizawai* serotype, which has additional toxins. Although reports indicate a lack of cross resistance between some serotypes of *B. thuringiensis* and thereby offer some hope for managing resistance to this bacterium, limiting selection pressure to any of the toxins will be necessary if *B. thuringiensis* is to remain a durable insecticide complex. We should be warned by the work of Jansson & Lecrone (82) who reported that although genetically improved strains of *B. thuringiensis* were effective in managing diamondback moths during the first two years of a study in Florida, efficacy declined markedly in the third year.

Integrated Pest Management

For the past 30 years, farmers have depended exclusively on insecticides to control diamondback moths, but resistance to presently available insecticides and lack of new insecticides has stimulated research on alternate control measures. In some cases, these alternatives are essentially the same ones that were discarded in favor of synthetic insecticides. Since parasitoids play such an important role in checking diamondback moth population growth, introduction and conservation of parasitoids will be basic to any sustainable IPM program. To implement IPM, growers must coordinate their efforts because practices of one grower influence those of his neighbor. This applies to the development of insecticide resistance or the introduction and conservation of natural enemies. Such coordination will be most needed in small-scale agriculture where farms are often <0.1 ha and where many farms in an area are owned by different growers. An example of a successful coordinated effort was the establishment of *D. semiclausum* in the highlands of Indonesia, Malaysia, Taiwan, and the Philippines and the conservation of the parasitoid with *B. thuringiensis* (119, 127, 143, 169). A similar successful program based on introduction and conservation of natural enemies was developed in Missouri (K. D. Biever, personal communication). An IPM project funded by the Asian Development Bank will soon cover all countries in South and Southeast Asia where, if not already present, *D. semiclausum* will be introduced in the highlands and *C. plutellae* in the lowlands. In the lowland areas of the tropics and subtropics where temperatures are high, *C. plutellae* is the only larval parasitoid that can survive. Although this parasitoid has been established in several crucifer-growing areas in the tropics and subtropics (171, 176), this parasitoid alone is not effective in controlling diamondback moth and supplemental measures are required. Certainly one of the most successful IPM programs is the one developed in the Bajio region of Mexico where ~15,000 ha. of crucifers are grown annually. This program was initiated in 1987 after a complete control failure of diamondback moths despite an

average of nine applications of synthetic insecticides. The present IPM program in 1992 relies on scouting thresholds, crop-free periods, and the judicious use of Bt, and has resulted in >50% fewer insecticide sprays (J. A. Laborde, personal communication).

In areas where other pests besides diamondback moths are important, one must consider their management as well. For example, *Crociodolomia binotalis* is a major pest of crucifers in the highlands of Indonesia, and presently marketed strains of *B. thuringiensis* are not effective against it. Growers who have used synthetic insecticides routinely against *C. binotalis* have caused occasional flareups of diamondback moths because of insecticide-induced mortality of *D. semiclausum* (144). Throughout much of North America, cabbage is also attacked by imported cabbageworm, *Artogeia rapae*, cabbage looper, *Trichoplusia ni*, onion thrips, *Thrips tabaci*, and cabbage aphid, *Brevicoryne brassicae*. Presently, only commercial control of onion thrips can be accomplished using host plant resistance (150, 157), and *B. thuringiensis* is not effective against aphids and is only marginally effective against cabbage looper. Other control tactics that are compatible with diamondback moth control must be developed for these pests.

Because of the magnitude of control failures of the diamondback moth, as well as the pressure to reduce insecticide input in small- and large-scale agriculture, both systems must be open to alternatives to broad-spectrum insecticides. Traditionally, such ideas as trap cropping, adult trapping, and pheromone disruption were considered more amenable to small-scale agriculture, but this is no longer true. Researchers in India have demonstrated the benefits of using a mustard (*B. juncea*) trap crop to attract diamondback moths away from the principal crops (154), thus reducing the need for insecticides to a maximum of two sprays compared with 10 or more per season for conventional control methods. A team of Thai and Japanese scientists has demonstrated the utility of yellow sticky traps to capture diamondback moth adults, thereby reducing their oviposition and subsequent damage by larvae (137). In fields with such traps, three sprays of *B. thuringiensis* achieved better control and twice as much crop yield as five sprays of *B. thuringiensis* mixed with mevinphos in a check field. Combining mustard trap cropping and yellow sticky traps may reduce the need for insecticides even more. In Japanese field tests of mating disruption by pheromones, populations of diamondback moth have been reduced by 95% compared with control fields (116). Preliminary tests in Florida have not been as successful, but pheromone disruption may still serve as an important component along with parasitoids and *B. thuringiensis*.

The concept of sampling populations and treating when thresholds are exceeded is fundamental to IPM and has been promoted in developed countries (15, 21, 75, 76, 146, 149, 179) and in many developing countries of the

tropics (23, 24, 95, 137, 142). This strategy's adoption, however, is hindered because it requires regular scouting by trained personnel who may not be available. In developing countries, adoption of IPM is also hindered because many farmers cannot differentiate pests from beneficials, some farmers have difficulty in counting because of their illiteracy, and resistance to multiple insecticides makes most insecticide applications useless. Thus, in the tropics and subtropics, community-wide management will most likely rely primarily on the release and establishment of as many parasitoids as possible and the use of cultural practices.

SUMMARY AND CONCLUSIONS

In the past 40 years, the diamondback moth has become one of the most difficult insects in the world to control because of its intrinsic biology and ecology and its large host range, which includes many crops that have high cosmetic standards. Central to control failures is the development of resistance by diamondback moths to every insecticide that has been widely used against them, including *B. thuringiensis*. Because of insecticide resistance, concern for insecticide residues on the crop and in the environment, and deleterious effects of synthetic insecticides on natural enemies, alternatives to the regular use of synthetic insecticides are sorely needed.

Parasitoids, especially *D. semiclausum* and *C. plutellae*, have been tremendously successful in controlling diamondback moth populations in the highlands and lowlands, respectively, in Southeast Asia and provide a model for the basics of a successful IPM program. Importation of these or functionally similar biological-control agents can serve as the basis of a management program, but this will require a switch to insecticides that are compatible with natural enemies. Use of *B. thuringiensis* in this context has proven successful in several parts of the world, but the isolated cases of resistance to *B. thuringiensis* warn of future problems. How stable this resistance is and what the potential is for cross-resistance between toxins of various strains, isolates, and serotypes are questions that must be addressed if *B. thuringiensis* is to remain a viable tool for diamondback moth management.

Past experiences with diamondback moth management have reinforced the belief that single-component strategies will fail. New technologies such as host-plant resistance, development of new pathogens and insecticides, and mating disruption with pheromones must become available to complement our traditional strategies of biological control, trap crops, host-free periods, and the like. Because of the importance of crucifers in the human diet and local and world economies, entomologists will continue to be challenged to develop rational and sustainable management systems for diamondback moths.

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CONTENTS

PHYSIOLOGICALLY INDUCED CHANGES IN RESOURCE-ORIENTED BEHAVIOR, <i>L. Barton Browne</i>	1
MANAGEMENT OF GENETICS OF BIOLOGICAL CONTROL INTRODUCTIONS, <i>K. R. Hopper, R. T. Roush, and W. Powell</i>	27
BIOLOGY AND CONTROL OF CATTLE GRUBS, <i>Philip J. Scholl</i>	53
BIONOMICS OF THRIPS, <i>T. N. Ananthakrishnan</i>	71
PLANT COMPENSATION FOR ARTHROPOD HERBIVORY, <i>J. T. Trumble, D. M. Kolodny-Hirsch, and I. P. Ting</i>	93
BIONOMICS OF THE BRACONIDAE, <i>R. A. Wharton</i>	121
INSECTS IN AMBER, <i>George O. Poinar, Jr.</i>	145
COMPARATIVE ENDOCRINOLOGY OF MOLTING AND REPRODUCTION: Insects and Crustaceans, <i>Ernest S. Chang</i>	161
ENTOMOPATHOGENIC NEMATODES, <i>Harry K. Kaya and Randy Gaugler</i>	181
BIOSYSTEMATICS OF THE HELIOTHINAE (LEPIDOPTERA: NOCTUIDAE), <i>Charles Mitter, Robert W. Poole, and Marcus Matthews</i>	207
A MULTIFUNCTIONAL ROLE FOR OCTOPAMINE IN LOCUST FLIGHT, <i>Ian Orchard, Jan-Marino Ramirez, and Angela B. Lange</i>	227
INSECT BEHAVIORAL AND MORPHOLOGICAL DEFENSES AGAINST PARASITOIDS, <i>Paul Gross</i>	251
BIOLOGY, ECOLOGY, AND MANAGEMENT OF THE DIAMONDBACK MOTH, <i>N. S. Talekar and A. M. Shelton</i>	275
GEOSTATISTICS AND GEOGRAPHIC INFORMATION SYSTEMS IN APPLIED INSECT ECOLOGY, <i>Andrew M. Liebhold, Richard E. Rossi, and William P. Kemp</i>	303
NEUROENDOCRINE CONTROL OF SEX PHEROMONE BIOSYNTHESIS IN LEPIDOPTERA, <i>Ashok K. Raina</i>	329
MYRMECOMORPHY: Morphological and Behavioral Mimicry of Ants, <i>James D. Mclver and Gary Stonedahl</i>	351

COMPARATIVE GENETIC LINKAGE MAPPING IN INSECTS, <i>David G. Heckel</i>	381
DIVERSITY IN THE NEW WORLD MEMBRACIDAE, <i>Thomas K. Wood</i>	409
INDEXES	
Subject Index	437
Cumulative Index of Contributing Authors, Volumes 29–38	447
Cumulative Index of Chapter Titles, Volumes 29–38	450